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Wilby, Andrew & Hector, Andy
Andrew Wilby, Lancaster University, Lancaster, Lancashire, UK
Andy Hector, University of Zürich, Zürich, Switzerland

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Abstract

Human activities have caused widespread loss of biodiversity raising concern about the potential impact on ecosystem processes (flows of energy and materials). A large body of recent research has shown that as species are lost from ecosystems there is, generally, a minor impact on ecosystem processes, but that this impact increases disproportionately as species diversity declines. Functional complementarity among species, due to variation in the ecological niches occupy, appears to be the main mechanism driving this pattern. Species diversity is also usually positively related to ecosystem stability i.e. their variation through time and the resistance and resilience to perturbation. These findings are already powerful arguments for the conservation of biodiversity, though current research aims to increase their relevance to the real world by including a more extensive range of ecosystems and processes, realistic food web structures, realistic (non-random) extinction scenarios and larger spatial scales.

Key Words

Ecosystem functioning; ecosystem stability; species diversity; conservation biology

Contents

Introduction

Human activities have caused dramatic changes to the variety and distribution of organisms across the globe, both through the introduction of species to regions where they formerly did not exist and through the degradation of biological communities. These effects, which have accelerated in modern times, have led to changes in biological diversity (often shortened to *biodiversity*) defined by the Convention on Biological Diversity (CBD) as the *"variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems".* Under this definition, biodiversity encompasses the rich variety of biological entities at a range of biotic scales from genes through species to complexes, such as ecological communities (groups of interacting species) or ecosystems (groups of interacting species and the physical processes they interact with). Biodiversity can also have several components: the number of different entities (often termed '*richness*' e.g. of genotypes, species, or ecosystems); the relative abundances of these entities; and their functional characteristics or interactions. Although humanity has influenced all these components of biodiversity, studies of the effects of biodiversity loss commonly attempt to isolate the effects of changes in richness (usually the number of different species) or functional attributes from those due to changes in relative abundance

The CBD was a response to concerns that biodiversity loss would compromise a range of benefits, often called *Ecosystem Services*, that humanity derives from biodiversity. This concern has also led to renewed scientific interest in the ecological value of biodiversity, and a concerted effort by ecologists to understand the ecological effects of changes in biodiversity. In particular, this research has focussed on the effect of altered biodiversity on the way ecosystems function, i.e. the processing of energy and materials though biological entities, and the likely significance of such changes for humankind. Here we summarise the conclusions of this recent research and current knowledge about the mechanisms underlying the relationship between biodiversity and ecosystem functioning. **See also:** Conservation Biology and Biodiversity.

Ecosystem functioning

Ecosystem functioning encompasses a broad range of phenomena including the provision of services by ecosystems. In ecological studies, the term is more specifically applied to ecosystem processes, including the size of certain stocks or ecosystem compartments (e.g. pools of carbon, nitrogen or organic matter; or biomass of primary producers or consumers) or the rates of flow of materials and energy (e.g. primary production, fluxes of carbon between trophic levels) or ecological processes (e.g. or rates of prey consumption).

The advantages of species diversity have been long recognised in agriculture where intercropping and crop rotations have been used for thousands of years to improve the productivity and stability of yield. In *The Origin of Species*, Darwin was the first to formally recognise the role of diversity in ecosystem functioning by suggesting that niche space is more fully occupied in more diverse communities leading to higher productivity. Since the early 1990s there has been an explosion of empirical and theoretical research on this relationship and this has led to a much deeper understanding of the mechanisms linking biodiversity to ecosystem functioning. The mechanism proposed by Darwin is now referred to as *functional complementarity* and requires that different species occupy different niches (resource-use differentiation), such that the more species that are present the greater the efficiency with which the total niche space is used and the greater the rate of ecosystem processes such as primary production. If species occupy exclusive niches with negligible overlap with other species (perfect complementarity) then we expect ecosystem functioning to increase steadily as species diversity increases. The opposite scenario would occur where niches overlap considerably, in which case functioning increases markedly with diversity at very low diversity levels but rapidly saturates. Where there is little increase in function with increasing diversity species are said to be functionally redundant (Figure 1a). **See also:** Coexistence.

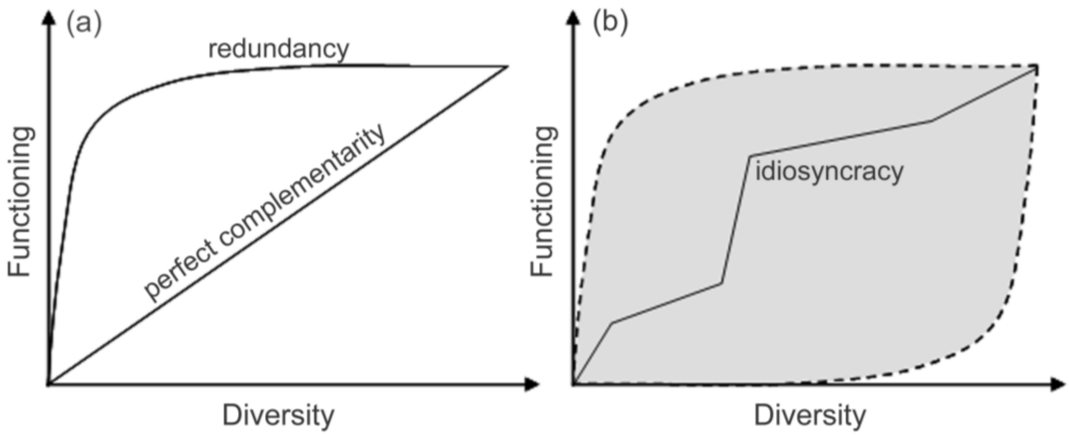

Fig. 1 (a) The influence of functional complementarity (non-overlapping niche space) and redundancy (overlapping niche space) on the shape of the diversity – ecosystems functioning relationship; and (b) differences among species in their impact on a function lead to an idiosyncratic relationship depending on the actual order of species assembly. The relationship can take a variety of trajectories within a broad envelope of response (the shaded area) depending on assembly order.

However, other mechanisms may also underlie positive relationships between species diversity and functioning. For example, increasing species diversity can also lead to increased functioning if there are synergistic interactions (facilitation) among species, where the functioning of one or several species is increased in the presence of others. For example, this may occur if one species increases the supply of resources to another, or if one species moderates environmental conditions to the benefit of another species. In experimental studies, facilitation and resource-use differentiation are sometimes grouped together under the term *functional complementarity* because it has often been impossible to distinguish between these mechanisms in experimental data.

Other closely related mechanisms linking diversity and function have been termed the *selection* or *sampling effects*. In any community, species are likely to vary in the extent that they influence a particular function; some plant species, for example, are intrinsically much more productive than others and in the right environmental conditions, they will come to dominate the community. In this situation, ecosystem functioning will be dependent on the composition of the community rather than its diversity per se. If this is the case, then a given scenario of species diversity will result in an idiosyncratic trajectory within a broad envelope of potential response depending on the order that species are added or removed from the community (Figure 1b). The *sampling* effect argues that high diversity communities are more likely to contain those species which have a large impact on functioning, leading to an overall positive relationship between diversity and functioning when these species dominate. The more general *selection effect* recognises that the reverse may also be true: species of lower biomass may dominate communities resulting in a negative selection effect.

The main approach used in experimental studies to test the dependence of ecosystem functioning on biodiversity has been the assembly of model communities of differing species diversity (or occasionally functional or genetic diversity) in laboratory or field. An alternative, but less common approach is to remove species from natural communities. Meta-analysis of the experimental studies since the early 1990s clearly shows that, overall, there is a positive relationship between species diversity and ecosystem functioning; and that this pattern is consistent across trophic groups and across terrestrial and aquatic ecosystems. Generally, the relationship is steep at low species diversity, but saturates at higher levels. Viewed in reverse, this relationship suggests that as species diversity is lost the impact on ecosystem functioning may initially be slight, but it will increase disproportionately at species diversity declines further. Since the expansion of studies of biodiversity and ecosystem functioning in the early 1990s there has been considerable debate about whether these observed positive effects of diversity on functioning resulted from functional complementarity or from sampling/selection effects. Statistical tests have been developed that can distinguish between these two types of mechanism given appropriate experimental design. These show that while species do vary considerably in their influence on ecosystem functioning, communities are often dominated by species which are not the most productive leading to negative selection effects. Negative selection effects have been shown to be almost as common as positive selection effects. Hence, functional complementarity (niche-differentiation or facilitation) appears to be the major mechanism underlying observed positive diversity – functioning relationships.

Despite the importance of functional complementarity, the finding that there is great variation among species in their impact on ecosystem processes is key to the interpretation of experiments and application of biodiversity – ecosystem functioning theory. Most experimental studies randomly remove species from communities, and there has been criticism that species are not lost randomly in nature. Where large variations occur in the impact of species on functioning, the effect of biodiversity loss on functioning will depend strongly on the order in which species are lost (Figure 1b). As we will see later, incorporation of more realistic scenarios of species loss is a key component of the next phase of research that will help inform strategies for biodiversity conservation in the real world.

Productivity gradients

As explained above, research of biodiversity on ecosystem functioning has largely used two methods to manipulate diversity: the experimental removal of species (removal experiments) or the assembly of experimental communities of varying diversity. A third possibility is to use an observational approach look at the co-variation between biodiversity and ecosystem functioning in nature. In fact, there is a long tradition of using this approach to examine the effects of productivity (an ecosystem process) on diversity. Note that the inferred causation is reversed here relative to the biodiversity experiments: the idea is to examine how productivity controls diversity not how diversity influences productivity. Not surprisingly, this has led to some confusion and controversy. While the frequency of different types of patterns in the relationship between productivity and diversity (positive, negative, unimodal etc.) and their causes are still the subject of debate, diversity is often positively correlated with productivity at large-scales (from regional to global). At smaller scales a variety of inter-relations are seen including negative, unimodal and null relationships. **See also**: Species Richness: Small Scale.

Species number or functional groups?

The mechanisms resulting in positive species diversity – ecosystem functioning relationships (functional complementarity) are dependent on species differing in their functional niche. This has led to the idea that looking at the diversity of functional characteristics (functional diversity) of the organisms in a community may lead to better predictions of ecosystem functioning than species, or more generally, taxonomically based measures of diversity. In the first phase of experiments, this was done by grouping species into functional groups based on their similarity of growth form or physiology and testing for any influence of functional group richness on the ecosystem process under study. These early experiments did show positive relationships between functional group richness and ecosystem functioning, in particular the important role of legumes (nitrogen fixing) and non-legumes in driving plant community biomass production. Generally, these studies show that complementarity and facilitation are greatest when species differ greatly in the functional traits they possess. While functional group richness does explain a portion of the influence of biodiversity on ecosystem functioning, there is also evidence of finer scale functional differences among species within functional groups which lead to positive effects on ecosystem functioning.

In recent times, there have been attempts to define the functional diversity of communities more explicitly than in the designation of functional groups using continuous measures of functional diversity. Several methods have been developed that allow the measurement of functional diversity using the traits of the constituent species of a community. Species are characterised against a list of traits of known or suspected functional significance and functional diversity is calculated by one of several methods to represent the total distances between species in trait space. Initial results tend to confirm that such measures of functional diversity tend correlate more closely with ecosystem functioning than species diversity or functional group richness.

Multi-trophic systems

Much of the work on biodiversity – ecosystem functioning relationships has been done on plant or microbial communities, often encompassing only single trophic levels. Moreover, much of the underlying theory concerning complementary resource-use was derived from communities in which species coexist through niche complementarity. We should not necessarily expect the same patterns of diversity – functioning in systems which are either highly disturbed or where populations are limited by the top-down control by predators, rather than by the availability of resources. While dominated by studies on plant or microbial communities, recent meta-analyses do show that increased species diversity at a particular trophic level is associated with increased biomass (standing stock) at that level and increased depletion of resources at the lower trophic level, suggesting that patterns are general across trophic levels.

There is a relatively long history of study, much of it from the agricultural literature, of the cascading impact of plant diversity on the diversity and abundance of herbivores and the predators and parasites that prey on them. Hypotheses have been proposed which suggest that herbivore populations should be reduced as plant diversity increases because specialist herbivores find it harder to locate their food plants and because a higher diversity of predators and parasitoids is expected to be supported in more diverse plant communities. While there is evidence in support of these hypotheses, there are a substantial minority of studies which do not show the predicted pattern of response; the identity of plant species seems to be of greater importance than plant diversity per se in determining herbivore load. In addition, most of the large experiments which have manipulated plant species diversity have also monitored the response of herbivores and their predators and parasites. These studies show, generally, that as plant species richness increases, the species richness (but not the abundance) of herbivores increases, as does that of predators and parasites. Interpretation of these patterns is complicated by the feedback effects which cascade back down the food web. For example, although herbivore diversity may increase with increased plant diversity the change is buffered by the changes in the predator and parasite communities, which feedback to affect the herbivore community. Similarly, there are also likely feedback effects of herbivore community changes on plant diversity itself.

If biodiversity ecosystem functioning theory is to become more realistic then more multi-trophic studies, in which biodiversity loss and/or its impact is observed at several trophic levels, must be undertaken. The increased complexity caused by the incorporation of additional inter-specific interactions as we move up food chains makes prediction of diversity – functioning relationships much more difficult. Many of the experiments which have attempted to manipulate biodiversity at several trophic levels simultaneously have found idiosyncratic results, suggesting that prediction may be very difficult in all but the most simple food webs.

Some progress in describing cross-trophic level effects has been seen in the study of species diversity in predator – prey systems. This effort has arisen independently out of the realms of biological control and predator – prey research, where it is useful to know whether multiple predator species have a larger impact on prey populations than single species. One of the differences between these two bodies of work is that predator – prey studies explicitly deal with direct and indirect inter-specific interactions among species in the target community and how they might affect functioning. By contrast, biodiversity – ecosystem functioning theory is based on niche overlap (which is implicitly based on competitive interactions in evolutionary history). In predator – prey systems, intra-guild predation, where one predator feeds on another predator rather than the prey in the trophic level below, is a very common phenomenon. Increasing chance of intra-guild predation as species diversity increases is a mechanism that can result in a negative relationship between predator diversity and prey population suppression. In addition, individuals of a particular species may change their behaviour when they encounter another species, which may either increase or decrease ecosystem processes or have no effect depending on the context. At higher trophic levels at least, we have mechanisms driving negative or neutral diversity – functioning relationships that may operate alongside, and possibly counter-act the positive effects of functional complementarity. As discussed above, meta-analysis has revealed that there is a general positive relationship between diversity and a range of ecosystem processes, but if the studies of terrestrial predator-prey systems are considered in isolation, the results are much less clear-cut, with some studies showing positive relationships, but an equal number showing negative or neutral effects of increasing predator species diversity on prey suppression. In such systems it is apparent that observed diversity effects are potentially the net result of several concurrent mechanisms some leading to positive and some to negative relationships. A current focus of research is to understand when and why positive or negative mechanisms dominate.

Effects on stability

In addition its role in the rate of ecosystem processes, biodiversity is also hypothesised to be a key factor in the stability of ecosystems. For much of the last century, the adage "diversity begets stability" was an accepted part of ecological wisdom. Largely anecdotal evidence of Elton in the 1930s and the conceptual models of MacArthur and Odum in the 1950s supported the view that diverse ecosystems are more stable. Several mechanisms were proposed for this link: compared with simple communities, diverse communities have more routes for energy to flow; more interactive links between species; more negative feedback loops to control outbreaking populations; and more species capable of taking over the role of other species than low diversity communities. Despite the apparent logical consistency of these models, and the prevalence of anecdotal information to support them, rigorous mathematical investigation of the stability of simulated communities in the 1970s began to raise contradictory predictions concerning the influence of diversity on stability. A controversy arose resulting in a plethora of studies aimed at resolving the question of whether diversity does indeed promote stability in ecosystems.

Part of the inconsistency in prediction of the relationship between diversity and stability was due to imprecise definition of the term stability. Stability, which itself has several different attributes, has been used with respect to both the species composition of communities and also to their functioning. Mathematically speaking, the stability of a system is a measure of its ability to return to equilibrium following perturbation. Systems are globally stable if they return the equilibrium state following any perturbation irrespective of its strength, or locally stable if they return so long as the perturbation is not too severe. The application of these abstract mathematical concepts to real ecological systems has been problematic as it is often difficult to identify the equilibrium state with precision, if indeed equilibrium exists. Generally, in ecological systems, stability relates either to the response to perturbation or to the temporal variability of an attribute through time. When referring to the response to perturbation, two different components of stability are commonly identified: resistance and resilience. Resistance refers to the extent that the perturbation influences the community (the induced change in composition or functioning) and resilience refers to the ability of the community to recover its pre-perturbation state.

There are several formal mechanisms which have been hypothesised to underlie diversity – stability relationships, some of which are formalisations of the logical arguments proposed in the 1950s. The *Insurance Effect* argues that although high species diversity may encompass functional redundancy at any point in time, this high diversity may buffer the community against environmental change. The more species that are present in a community the greater chance that species are present which can maintain functioning in the face of perturbation. A related concept is the *Portfolio Effect* (named in analogy to stock market portfolios). This concept recognises that if species vary independently through time then the variability of the whole community will be less than the average variability of the constituent species (as long as species dynamics are not synchronised), similar to the way that a more diversified stock portfolio is a safer investment. *Compensatory dynamic effects* take this argument a step further in suggesting that where communities are structured by competitive interactions, dynamics of competitor species are expected to negatively co-vary i.e. when one species increases its competitor should decrease. This would force population asynchrony and decrease the variability through time of the aggregate community (Figure 2).

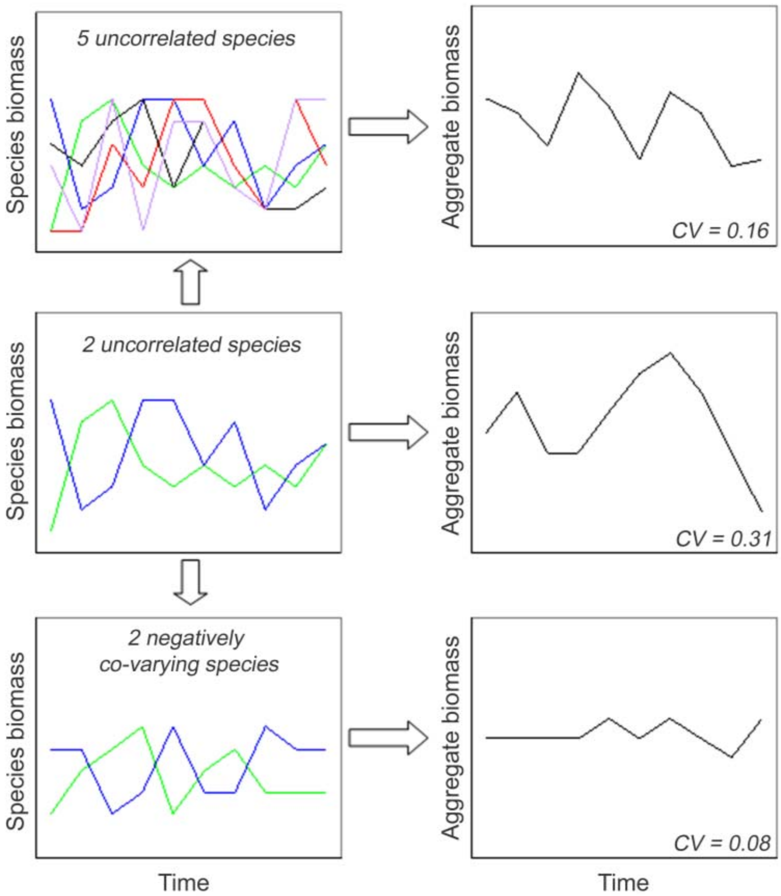

Fig.2 Mechanisms underlying diversity – stability relationships: increasing species richness results in more stable (reduced temporal variability, here measured as the coefficient of variation *CV*) community attributes, such as total community biomass, as long as there is some asynchrony, a mechanism termed the *portfolio effect*. Negative covariance in species abundances, which is expected in communities of strongly competing species, also has a stabilising effect on community attributes, sometimes termed the *negative covariance* or *compensatory dynamics effect*.

Many empirical tests of the effect of diversity on the stability of ecosystem functioning have been made in recent years, mostly involving the experimental manipulation of species diversity, and the majority of these studies produce results that are consistent with the notion that increased diversity means less variability of aggregate community functions. However, like studies of biodiversity and ecosystem functioning, most of these studies are of grassland / herbaceous or microbial communities and many focus only on a single trophic level. Most studies also only consider one or several of range of possible aspects of ecosystem stability. Generally, most experimental studies do support the notion that diversity begets stability, but a sizable minority do not. This suggests that despite the growing evidence we should exercise some caution before concluding that this is a general relationship.

One of the important realisations from recent experimental and theoretical research is that stability in an aggregate process, such as the productivity of a whole community, does not necessarily require that the contributions of each individual species to the process are equally stable. For example, long term experimental studies have shown that in plots with higher species diversity the temporal variation in total primary production is reduced compared with communities of lower species diversity. However, the variability in productivity of individual species tends to increase with increasing species diversity. In other words, community stability and population stability respond in opposite directions to increasing species diversity (Figure 3). **See also:** Food Webs; and Species Richness: Small Scale.

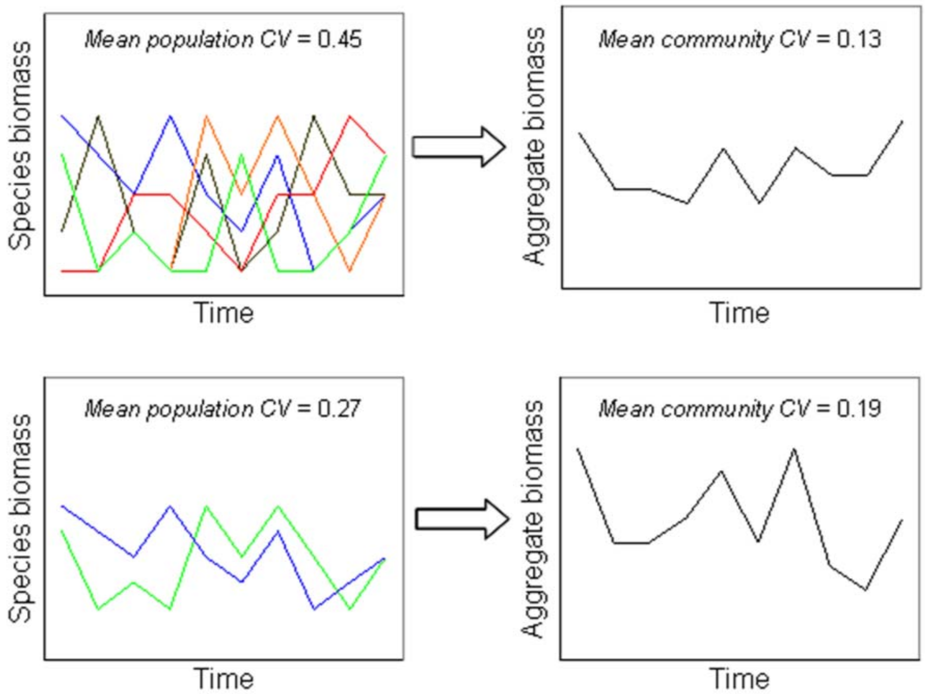

Fig. 3 Contrasting responses of population and community stability to increased species richness. In moving from the bottom panel to the top panel, species richness increases from two to five and mean temporal variability in biomass of the populations increases. However, the community stability (aggregate biomass) increases due to averaging effects.

Ecosystem multi-functionality

As discussed above, meta-analyses of experimental data to date suggest that there is a positive but saturating relationship between biodiversity and individual ecosystem processes. The saturation of this curve suggests that at high levels of biodiversity species are functionally redundant to some extent. However, most studies only address one or a small number of ecosystem processes over relatively short periods of time and under a restricted and often controlled set of environmental conditions. In order to relate biodiversity – functioning theory to real ecosystems and to understand how biodiversity loss is expected to impact on ecosystem stability and service provision, we must take a broader perspective on the functional importance of biodiversity; how does the full range of vital ecosystem processes in the longer term respond to biodiversity change?

To some extent, work on the insurance effect, as discussed above tells us about the value of biodiversity in buffering against the environmental changes that occur over longer time scales, so our expectation is that biodiversity effects on function will be more evident over time. Evidence from Tilman's long term diversity experiment in Minnesota does suggest that higher diversity treatments have lower temporal variability in production. Together with the general positive effect of complementarity on production, we might conclude that higher diversity communities have a higher long-term average, and less variable, productivity.

If we turn to studies which explicitly focus on a range of ecosystem processes driven by a community, information is severely lacking. However, one study has looked at seven ecosystem processes across a network of eight grassland diversity experiments distributed across Europe (See Hector & Bagchi (2007) in Further Reading). This study supports the hypothesis that the greater the number of ecosystem processes considered, the greater the number of species found to affect overall functioning (Figure 4).

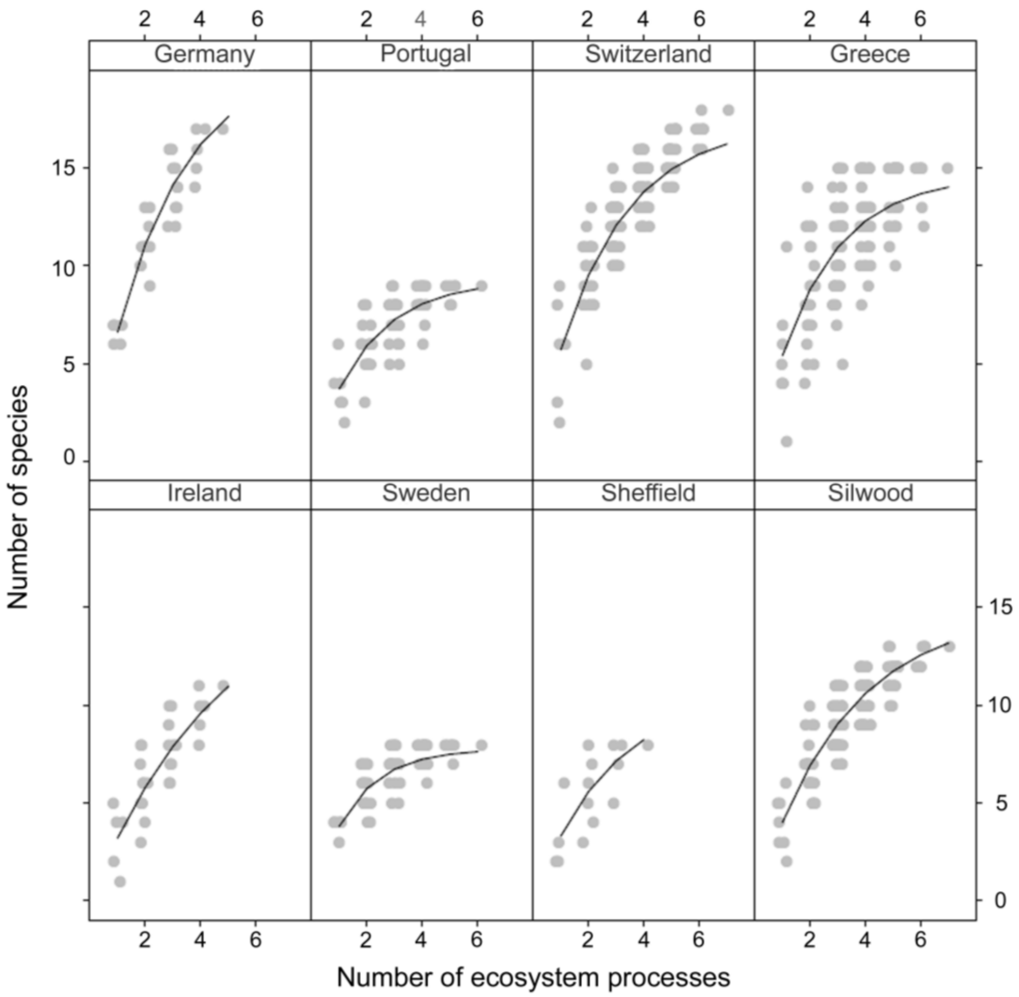

Fig. 4 Ecosystem multifunctionality requires higher levels of diversity than single functions alone. Grey points show numbers of species required for all possible combinations of ecosystem processes and lines are predictions based on the mean number of species required for a single process and the average overlap in the sets of species required for each pair of processes (see Hector & Bagchi 2007 in Further Reading).

Consequences for conservation biology

The maintenance of ecosystem functioning is just one justification for conservation of biodiversity, alongside a range of other justifications based on its intrinsic (inherent value not related to its utility to humankind) or utilitarian values based on cultural (aesthetics, psycho-spiritual values) or direct use values. That said, ecosystem functioning is an important and effective justification for biodiversity conservation, perhaps because of the relative ease (in principle) of quantifying the relationship between diversity and function hence in quantifying the value of biodiversity in tangible terms.

One reported danger of using diversity – function relationships to justify conservation is that while the positive relationship between diversity and function is apparently general, the relationship tends to saturate at around half the maximal level of diversity. This has been interpreted as an indication that we can afford to lose around half of our species before we expect to see substantial negative impacts on ecosystem functioning. Several arguments can be found to counter this interpretation. Firstly, while we know that functioning can be maintained under considerable diversity loss, the impact of diversity loss is extremely variable due, in part, to differences among species in their influence on processes. It is not clear at present for any process that we can identify which species are required to maintain functioning, and even if we could, we do not generally have control over the species which are lost from ecosystems as their diversity declines. Second, the insurance hypothesis indicates that species that appear functionally be redundant at one point in time may not continue to be redundant if environmental conditions change. Indeed, niche theory would predict that true redundancy can not persist in natural systems as the dominant species would competitively exclude all other species with identical niches. Thirdly, extinctions can precipitate further extinctions of closely interacting species. This means that allowing some diversity may result in cascading losses of other species reducing biodiversity below the threshold at which function is impaired. Finally, most asymptotic relationships consider only a single ecosystem process or service and while the relationship may remain asymptotic the level of diversity to support multiple ecosystem functions seem to be generally higher.

In order for biodiversity – ecosystem functioning theory to better inform biodiversity conservation, three main challenges have been identified. First, much of our current understanding is based on experiments undertaken on single trophic levels. Real ecosystems contain multiple trophic levels and we must expand our theory to incorporate multi-trophic perspectives. Questions such has how higher trophic levels respond to increased productivity associated with increased plant diversity, how far such effects cascade through food chains and whether there are feedback effects on plant communities remain highly relevant.

Another challenge for the application of biodiversity – ecosystem functioning theory to conservation is that most experimental studies have been undertaken at small spatial scales whereas conservation policy and monitoring of biodiversity loss tend to be implemented at larger (regional) spatial scales. At present we know that diversity tends to be positively correlated at regional and local spatial scales but the mechanisms maintaining this correlation are not fully understood. We need to resolve whether maintaining or boosting biodiversity at regional levels will result in higher diversity and improved function at the local scales which have been the subject of most experiments.

Finally, one of the principal criticisms of biodiversity – ecosystem functioning theory to date is that experiments tend to simulate random species extinction, whereas in reality we know that species loss is unlikely to be random. If, for example, rare species are lost first in a given extinction scenario (e.g. extinction processes that lead to the loss of small populations), which seems a reasonable assumption, then the impact on functioning may be minor compared with a scenario where the dominant and more functionally active species are lost first. However, loss of rare species can also have a significant impact on functioning if the species has strong trophic or non-trophic links with other species (i.e. a keystone species) resulting in a trophic cascade. Theory, therefore, has to start to incorporate more realistic patterns of species loss (e.g. over-harvesting of fisheries and forests). To some extent this is already being done with attempts to identify traits or characteristics that render a species susceptible to extinction and asking whether these traits also have an influence on the functionality of the species in question.

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Glossary

- Biodiversity: A contraction of biological diversity that encompasses all biological variation from the level of genes, through populations, species and functional groups (and sometimes higher levels such as landscape units).
- Ecosystem functioning: An umbrella term for the processes operating in an ecosystem.
- Ecosystem processes: The biogeochemical flows of energy and matter within and between ecosystems, e.g. primary production and nutrient cycling.
- Ecosystem service: An ecosystem process or property that is beneficial for human beings, e.g. the provision of foods and materials or sequestration of carbon dioxide.
- Selection effects: The influence that species have on ecosystem functioning simply due to their species-specific traits and their relative abundance in a community (positive selection effects occur when species with higher-than-average monoculture performance dominate communities).
- Complementarity effect: The influence that combinations of species have on ecosystem functioning as a consequence of their interactions (e.g. resource partitioning; facilitation, reduced natural enemy impacts in diverse communities).